

SIEBOLD'S NEW RESEARCHES IN  
PARTHENOGENESIS \*

AMIDST the all-absorbing discussion of the problems which have arisen out of the general acceptance among biologists of the law of evolution, the phenomenon of Parthenogenesis which, previously to Mr. Darwin's work on the Origin of Species, excited the interest and called forth the investigations of observers in much the same manner as his theory has done of late years, has met with a reverse of fortune and fallen into a subordinate rank of popularity. The distinguished naturalist, however, who fifteen years ago gave so stunning a blow to current theories of the reproductive process, by demonstrating the occurrence in moths and bees of what he designated as "true parthenogenesis"—that is to say, the development, without impregnation, of an ovum capable of being impregnated—has not let the subject drop. Professor Siebold has made further experimental researches, establishing again, and on a larger basis, his former conclusion, and adding at least one new fact of great general importance for the understanding of the process of sexual reproduction. Although upon its first appearance in 1856, the conclusion arrived at in his "Wahre Parthenogenesis" was admitted by almost all competent naturalists to be thoroughly demonstrated, and beyond the reach of criticism; yet some more and some less eminent biologists have not been wanting to deny the *Lucina sine concubitu*, and have raised such objections as that of a possible error in the condition of the experiments depending on the exclusion of males from the supposed parthenogenetic female; and again, that these so-called females were not demonstrated "not to be hermaphrodites." Indeed so deeply rooted is the conviction that eggs are made to be impregnated by spermatozoa, and that they then, and then only, can proceed to develop, that Siebold felt it necessary to add to his proofs, in order to establish his position that not only do unimpregnated eggs develop into perfect animals, but that such an event is by no means an exceptional occurrence among certain groups, and has a definitely fixed and orderly recurrence amongst them. He naturally was also anxious to extend the class-limits within which a true parthenogenesis can be said to occur, and he desired to inquire into the sex of the parthenogenetically-produced offspring in such cases as could be critically and decisively studied. Hence the renewed researches which have extended over several years, and the results of which are given in the present brochure.

Von Siebold's merit in this and his former work (but more especially in this) is not the enunciation of a new theory, or hypothesis, but the great care, ingenuity, and persistence which he has displayed in investigating cases in which for many years collectors, bee-keepers, and such naturalists of the limited, or "gardener" type, had asserted reproduction by means of unfertilised eggs to take place. It must be remembered that he was himself a strong opponent in 1850 of the supposition which he has now shown to be justified in fact, and that Leuckart in his article "Zeugniß," in Wagner's Handwörterbuch, and in other publications, preceded him as an advocate for the existence of true parthenogenesis, endeavouring, by microscopical researches, to give a solid observational basis to Dzierzon's hypothesis. It was not until 1857 that Siebold published his observations on bees, demonstrating what had been previously supposed, viz., that the queen-bee exhausts her store of received sperm in fertilising eggs which give rise to females only, and that then she lays unfertilised eggs, which become drones only, whilst the unfertilised worker-females also lay eggs which give rise to drones, and again that in certain moths (*Psyche* and *Solenobia*) unfertilised ova develop and produce females only. Leuckart followed (1858) with his "Zur Kenntniß des Generations-wechsels und der Parthenogenesis bei den Insekten." In this work, whilst asserting his claims to the merit of first espousing the cause of true parthenogenesis, Leuckart gives an excellent view of the general signification of the phenomena, and insists on the importance of extended histological observation in the examination of alleged cases of parthenogenesis. In his present work Siebold cannot be charged with in any way neglecting this part of his subject, for he has given most important and minute descriptions of the generative organs of the two principal cases studied (*Polistes* and *Apis*), containing new facts. His method is however eminently experimental, and appears to us a striking contradiction of a very superficial classification of the sciences, which is favoured sometimes by men of science unacquainted

with the methods or problems of biology: we mean the division into the exact or mathematical, the experimental, and the classificatory sciences, in which last division the so-called natural history sciences are said to find their place.

The experiments which Siebold made on bees and wasps, though performed by a naturalist, are as nicely controlled, and as clear in the conclusions which they give, as any performed by exact physicists on the times or quantities concerned in this or that physical process. The style in which details of these investigations are communicated is one rare at the present day in biological works, where minute description of structure, or of the apparatus devised for a physiological research, form the staple. Here we are treated to a leisurely narrative of some years of patient work; we share the keen enjoyment of the author as he becomes acquainted with the marvellous intelligence of his wasps and their various proceedings—we feel his satisfaction in overcoming the difficulties of procuring and observing the necessary material, and admire the candour and thoroughness with which he handles the question before him.

Before proceeding to a short notice of the contents of Von Siebold's book, it will be well to give a brief statement of the signification which such inquiries as his have in the present state of knowledge. Harvey's dictum, "Omne vivum ex ovo," expressed a great law, which had to be qualified when the researches of Trembley and others made known, among Polyps, and Worms, and Protozoa, reproduction by fission. To this rapidly succeeded the recognition of a modified fission, in which the animal did not divide into equal parts, nor exhibit the power of reproduction of the whole animal in artificially detached portions of its body; but in which special sprouts or buds were found to be prepared and detached spontaneously, becoming then developed into perfect animals. This process received the name of gemmation, and was stated to occur in polyps and also in the plant-lice. Parallels for these methods of reproduction in animals were readily recognised in plants, in the multiplication by seed, by cuttings or shoots, and by separable buds. A broad line was drawn between "buds" and "eggs," however egg-like the former might appear, in the assumption that eggs were special bodies of a peculiar structure, destined to be "fertilised" by the spermatozoa of the male—after which process only could they develop. These distinctions, some twenty years ago, were the more firmly impressed in the minds of biologists by the then recently acquired knowledge of the process of fertilisation or impregnation. Then came the demonstration by Siebold of the capacity for development of true eggs, even when not impregnated. The sharpness of the limit between buds and eggs was by this at once destroyed; and the closely following researches of Leydig (antecedent to Siebold's work in some cases), Huxley, Lubbock, and Leuckart, on the structure of the supposed buds of Aphis and allied insects, and of lower crustaceans, proved that these bodies were morphologically ova—originating in ovaries, and having the essential structure of fertilisable ova. For them the term "pseudova" was introduced by Prof. Huxley, since they differ in this respect from other ova—that whereas the latter can be, and are in most cases (though with constant exceptions), fertilised, the latter cannot be.\* Whilst, then, up to this period such a thing as parthenogenesis appeared to be a strange exception, the question has now shifted, and, since the essential identity in reproductive power of cuttings, buds, pseudova, and eggs is proved, the problem before naturalists is rather, "Why are eggs ever fertilised?" in short, "What is the use of the male sex at all?" We have animals and plants multiplying by fission, breaking up into two or more parts, each of which becomes a new individual; we have them giving rise by growth to masses of cells, which become detached or remain attached, and develop each into a new individual; and finally, we have them elaborating single large cells, which become detached and develop each into a new individual. Why should it be that in certain cases these last require the fusion of another peculiar kind of cell elements before they will develop? Some light seemed to be thrown on this matter at first, by the observation that the unfertilised ova of the bee always produce drones, and that only the fertilised produce females; but this indication of a possibly clearer insight into the matter is entirely upset by the fact, now fully established in the present work, that in some species of

\* Leuckart has more recently proposed, in describing the reproduction of the Cecidomyia larvæ discovered by Wagner, to limit the term "pseudovum" to such ova as those produced by larvæ, or imperfect forms; and not to apply it at all to the eggs of bees, wasps, &c. (which can develop without fertilisation), as was done by Huxley. The falsity implied in the prefix seems to make a rather stronger distinction than is desirable between any of these bodies; for they are all truly ova, though ova of various special properties.

\* "Beiträge zur Parthenogenesis der Arthropoden." Von C. Th. E. von Siebold, Professor der Zoologie und Vergleichenden Anatomie in München. Leipzig: Engelmann, 1871.)

insects and crustaceans the unfertilised ova always, or in an enormously large proportion, produce females only; whilst in the Aphides we know that they ultimately produce both males and females. Mr. Darwin has suggested the most satisfactory theory of fertilisation, in assigning to it the object of fusing two life-experiences in the progeny, which thus gains tendencies and acquires impulses from a wider area than does an unfertilised ovum, and is in so far strengthened. Conjugation of two cells, similarly formed but belonging to different individuals (as seen in *Confervæ* and *Gregarinæ*) is the simplest arrangement for obtaining this end; the only difference between this and sexual reproduction is that in the latter process one cell seeks, the other is sought; and this differentiation into active and passive, the wooer and the wooed, commencing in the simplest vegetable and animal cells, persists to the highest rank of development. Self-impregnation (if it have a real physiological existence) and parthenogenesis, have, then, to yield, as chief modes of reproduction, to digenesis, or the concurrence of two individuals; and this for one and the same reason. Perhaps the apparently anomalous facts that an animal—or plant, as the case may be—develops elaborate motile zoospores and copulatory organs, merely to fertilise its own egg; and that other animals and plants develop peculiarly constructed large cells, of a kind apparently especially elaborated in the progress of the general evolution of life, to provide for fertilisation, yet which never are fertilised—are only to be explained as cases of persistent structures with modified function. In the former case, Monogenesis, being sufficient to or necessitated by the conditions of life, yet avails itself of the apparatus inherited from digenetic ancestors; whilst similarly, in the second case (*pseudova*), Monogenesis, having advantages for the particular case (and not being a common phenomenon in the group), instead of making its appearance through new organs, avails itself of the ovary inherited from digenetic progenitors. Thus the insignificant form of an ovum (unsignificant, that is, so far as monogeny is concerned) takes the place of the more obviously appropriate bud or fission-product. The phenomenon of Alternation of Generations, usually treated of in connection with parthenogenesis, should by experiment on the physical conditions accompanying its variations enable us to ascertain a great deal more than is at present known of what is the signification of the differentiation of male and female sexual elements; and it is from further study of this and of True Parthenogenesis that progress in this part of physiology may be expected.

To return to Siebold's researches. The greater part of the book is devoted to an account of the parthenogenesis observable in the wasp *Polistes*. Leuckart first recorded in his work already mentioned, that the workers of wasps, ants, hornets, and humble bees lay eggs, which in one case he followed to the development of a larva, but of which he was not able to determine the sex. Siebold determined to study a species of *Polistes* common in and around Munich, which he identifies with much care, and after reference to specimens and authorities from many lands, as *Polistes gallica* var. *diadema* Latreille. He gives a minute description of the characters of the females and males; the two kinds of the former (queens and workers) being only distinguishable by size—the workers in all external characters as well as in their generative organs being merely smaller queens, and fully capable of copulation and impregnation. In the beginning of May, in Munich, the *Polistes* queens which were born in the previous summer and impregnated then, commence each to build a nest. No queen who built in the former year survives to build a second time, and the young queens never make use of the old nests. The *Polistes* are very particular in choosing a warm sunshiny spot, sheltered from wind and rain, and as such spots are not too common, a new nest is often begun near the weathered remains of an old one. Walls and trunks of trees, often at such a height as not to be easily reached, are the sites chosen. When the queen has constructed fifteen or twenty cells, she lays eggs in them, and is very hard-worked in guarding her nest and in providing food for the larvae as they hatch. She feeds them on caterpillars and other soft insects, first removing the alimentary canal (as cooks take out the entrails of a fish), and carefully applying the morsel to the lips of each larva. This process takes some time for one "hand," and hence the first brood is longer in coming to perfection than later broods, in the rearing of which the elder progeny assist. In the middle of June the first lot make their appearance, all small females ready to assist their parent in the advancement of her enterprise. The later broods develop more rapidly and acquire larger size from being better nourished, and towards the end of June (no drones being as yet

born) the females which come forth are as large as the old queen; they may, however, be easily distinguished from her by their comparative freshness of colour and wing. Great care is displayed in guarding the nest. At night the queen goes to sleep after having carefully inspected each cell, taking up her position at the hinder side of the nest. If she is disturbed in the night, she takes another survey of her house before again going to sleep. In the daytime if disturbed she makes an immediate attack on the enemy with her sting, and then flies back to her nest. She can sting several times, since the barbs on her weapon are not too long to allow of its being withdrawn. Ants are amongst the most common of the many insect enemies of these wasps, and when one ventures into the nest, the whole colony sting it to death, and immediately throw the body out. Birds are, however, not thus to be got rid of, and destroy immense numbers of the nests, so that Siebold was obliged to protect those he wished to study with nets. The members of one nest are not allowed to remain in another, if by chance a stranger comes in she is hustled out at once by the wasps near the entrance. Siebold convinced himself of this by painting the thorax of a number of *Polistes* belonging to different nests with different colours. Only late in the year, when the wasps seem to be getting careless or tired of their incessant work did he find that one or two had got mixed in certain colonies, to which they did not rightly belong. Although there is this sharp discrimination of individuals, yet it was found that by substituting one nest for another whilst the queen was away, she could often be deceived, so as to make her enter upon the possession of the substituted nest as though it were her own. Siebold found this a very useful plan when he wanted to change the position or locality of a nest so as to bring it into a safer or more accessible spot, or when a nest which he had been observing was by some accident deserted, or when a nest in a favourable position was less forward in the development of its larvae than one less favourably situated. By making the nests moveable, and substituting the one for the other in the absence of the queen, he was able to save himself much trouble and loss. The nests were made moveable by removing them from their original support and firmly fixing them to boards which were then hung up in the original position. The queens were very anxious after this operation had been performed, investigating with great care the strength of the support and the cord by which the board was hung, and sometimes adding to it themselves additional strength. By degrees such moveable nests could be lowered a little bit each day from an inconveniently high position, or taking the nest in the night under a cover whilst all the wasps were in it, it could be removed from a distant locality to the Professor's garden; in such cases a certain proportion always came to grief by the desertion of the colony; and the queen was then sometimes found at work on the old site constructing a new nest. Although strangers are not admitted in a well-regulated *Polistes* nest, yet by carelessness or desertion the brood of one colony will sometimes be exposed to the attacks of the workers of another, who then make use of the unfortunate larvae to feed their own young. It frequently happens that workers who have once indulged in this kind of thing, become what are called "robber wasps," utterly demoralised, and actually undo the whole labour of a colony by dragging out the grubs which they were lately so carefully tending in common with their fellows, to feed the still younger larvae. When this condition of things has once begun in a colony it soon goes to ruin, and hence it is necessary to destroy any deserted *Polistes* nests in the neighbourhood of those under observation, lest by entering the former the members of the latter should get the bad habit of pulling grubs out of their cells, and proceed to do the same in their own nests.

The rain is a very constant source of destruction to *Polistes* colonies, drowning the young by saturating the cells with moisture. Light rain will not, however, do much harm. Whilst Siebold was endeavouring to remove some of the water from a nest which had been drenched in a shower, he was astonished to find the wasps themselves already busy at the work, putting their heads into the cells, sucking up the water, then passing to the edge of the nest and spitting out the fluid. In this way they are able to get rid of the effects of a wetting if it is not very severe. Though the *Polistes* feed their young exclusively with animal food, they yet appear to collect a sweet fluid which Siebold found in some cells, and which he thinks the workers take for their own enjoyment, since they were seen entering such cells and apparently sucking at the contents—in fact, taking a little refreshment in the intervals of their labour.

The development of the grub is carefully described by the author, and a "pseudo-nymph" stage is recognised intervening between the nymph and the pupa. The perfect insect bites off the lid of its cell, and comes out with perfect wings, deposits first of all a drop of urinary excretion, and makes a trial flight, then returns to take part in the labours of the colony. The cell is often used again for another egg. The first drones make their appearance with the beginning of July, an important fact for Siebold's experiments, for if the nest is to be used at all now is the latest moment; they have to be killed off, and all the remaining larvæ and pupæ destroyed—in order to secure a colony consisting solely of virgins. The drones play a pitiable part in the nest—sneaking about in the empty cells, and behind the comb, not till the month of August are their generative organs fully developed, and then they make their first approaches to the females. Their proceedings are minutely described, and it appears that they meet with many rebuffs from the busily-occupied workers of the hive, and that it is outside at a distance from the nest that their addresses are at length accepted by those of the larger females destined to become queens. Not all the large females appear to have this destiny, and none appear to leave the nest until all the brood has been brought through, when (about the beginning of October) the nests become deserted. Only a few flattened old virgin wasps remain, who are killed off by the frosts, whilst the young queens have married and sought out for themselves winter quarters. Siebold distinguished black-eyed and green-eyed drones, and speculates upon the signification of this difference.

Having ascertained these and other matters relating to the *Polistes* in far greater detail than we have been able here to indicate them, Siebold was prepared to make his experiment. In the nest from which he wanted an answer to these questions, "can unfertilised *Polistes* females lay eggs which will develop?" and if so, "of what sex will the parthenogenetically produced progeny be?" he proceeded to destroy the queen and all the eggs, larvæ, and pupæ in the cells with the greatest care as late as possible in the season, so as to have as large a colony as possible left, the limit of the time being given by the date of the appearance of the first drone. The queens thus taken were used for careful histological study of the generative organs, and since in all cases Siebold found the *receptaculum seminis* filled with moving spermatozoa, he was able to feel assured that he had really removed the queen in each case. We will merely direct the attention of those interested in histology to the minute description here given of the ovary, which in the main agrees with Leydig's, and of the *receptaculum seminis*, which in opposition to Leydig, on account of its nerve supply, Siebold holds to be contractile. After waiting some days Siebold had the gratification of finding the first eggs laid in the cells of several of the nests from which he had removed queen, eggs, and larvæ, and he felt convinced that they could only have been laid by the small virgin workers who alone tenanted the combs. The whole affairs of the colonies proceeded just as well as when the queens were there, and the virgins watched and worked with the same assiduity as had done their queen-mother. In some cases Siebold actually saw a worker deposit an egg, and such egg-laying workers, when anatomically tested, showed, firstly, in the presence of *corpora lutea* (the precise signification of which the investigator had ascertained by his histological studies of the ovary) that eggs had been extruded, and, secondly, in the complete absence of spermatozoa from the *receptaculum seminis*, that the insect was a virgin. Out of a hundred nests which he had begun to observe in one season, and out of one hundred and fifty in another, only some twenty or so in each case came through all the long series of accidents from weather, insects, birds, &c., to which they were necessarily exposed, and some of those which promised the best results and had cost the most pains came to a bad end in the very last days of the research. In order to determine the sex of the wasps born from the eggs laid by the parthenogenetic females, Siebold in most cases only allowed the development to proceed sufficiently far to enable him to recognise the sex by anatomical investigation. The dried skin, however, of such grubs as were found dead in their cells afforded sufficient evidence of the sex. In all cases the parthenogenetic offspring was without exception male. The queen-wasps as we have mentioned also late in the season lay eggs which produce drones, which are easily distinguished from the drones parthenogenetically produced by their larger size. It occurred to Siebold when he first ascertained that the queens produce drones that such drones might visit his virgin colonies, and thus his whole experiment be

invalidated. He was, however, reassured on this point by a nearer acquaintance with the *Polistes*; for such drones are not born till later than the period at which his small females laid their eggs, the former event taking place at the end of July, the latter at the beginning; and, furthermore, as we have noticed above, it is not till still later (August), when the experimental cells were long since all occupied with eggs, that the power and desire of sexual activity comes to these drones.

E. R. LANKESTER

(To be continued.)

### ON INSTINCT \*

WITH regard to instinct we have yet to ascertain the facts. Do the animals exhibit untaught skill and innate knowledge? May not the supposed examples of instinct be after all but the results of rapid learning and imitation? The controversy on this subject has been chiefly concerning the perceptions of distance and direction by the eye and the ear. Against the instinctive character of these perceptions it is argued that, as distance means movement, locomotion, the very essence of the idea is such as cannot be taken in by the eye or ear; that what the varying sensations of sight and hearing correspond to, must be got at by moving over the ground by experience. The results, however, of experiments on chickens were wholly in favour of the instinctive nature of these perceptions. Chickens kept in a state of blindness by various devices, from one to three days, when placed in the light under a set of carefully prepared conditions, gave conclusive evidence against the theory that the perceptions of distance and direction by the eye are the result of associations formed in the experience of each individual life. Often, at the end of two minutes, they followed with their eyes the movements of crawling insects, turning their heads with all the precision of an old fowl. In from two to fifteen minutes they pecked at some object, showing not merely an instinctive perception of distance, but an original ability to measure distance with something like infallible accuracy. If beyond the reach of their necks, they walked or ran up to the object of their pursuit, and may be said to have invariably struck it, never missing by more than a hair's-breadth; this, too, when the specks at which they struck were no bigger than the smallest visible dot of an *i*. To seize between the points of the mandible at the very instant of striking seemed a more difficult operation. Though at times they seized and swallowed an insect at the first attempt, more frequently they struck five or six times, lifting once or twice before they succeeded in swallowing their first food. To take, by way of illustration, the observations on a single case a little in detail:—A chicken at the end of six minutes, after having its eyes unveiled, followed with its head the movements of a fly twelve inches distant; at ten minutes, the fly coming within reach of its neck, was seized and swallowed at the first stroke; at the end of twenty minutes it had not attempted to walk a step. It was then placed on rough ground within sight and call of a hen, with chickens of its own age. After standing chirping for about a minute, it went straight towards the hen, displaying as keen a perception of the qualities of the outer world as it was ever likely to possess in after life. It never required to knock its head against a stone to discover that there was "no road that way." It leaped over the smaller obstacles that lay in its path, and ran round the larger, reaching the mother in as nearly a straight line as the nature of the ground would permit. Thus it would seem that, prior to experience, the eye—at least the eye of the chicken—perceives the primary qualities of the external world, all arguments of the purely analytical school of psychology to the contrary, notwithstanding.

Not less decisive were experiments on hearing. Chickens hatched and kept in the dark for a day or two, on being placed in the light nine or ten feet from a box in which a brooding hen was concealed, after standing chirping for a minute or two, uniformly set off straight to the box in answer to the call of the hen which they had never seen and never before heard. This they did struggling through grass and over rough ground, when not able to stand steadily on their legs. Again, chickens that from the first had been denied the use of their eyes by having hoods drawn over their heads while yet in the shell, were while thus blind made the subject of experiment. These, when left to themselves, seldom made a forward step, their movements were round and round and back.

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